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Biological Report 82(11.32)
March 1985

TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest)

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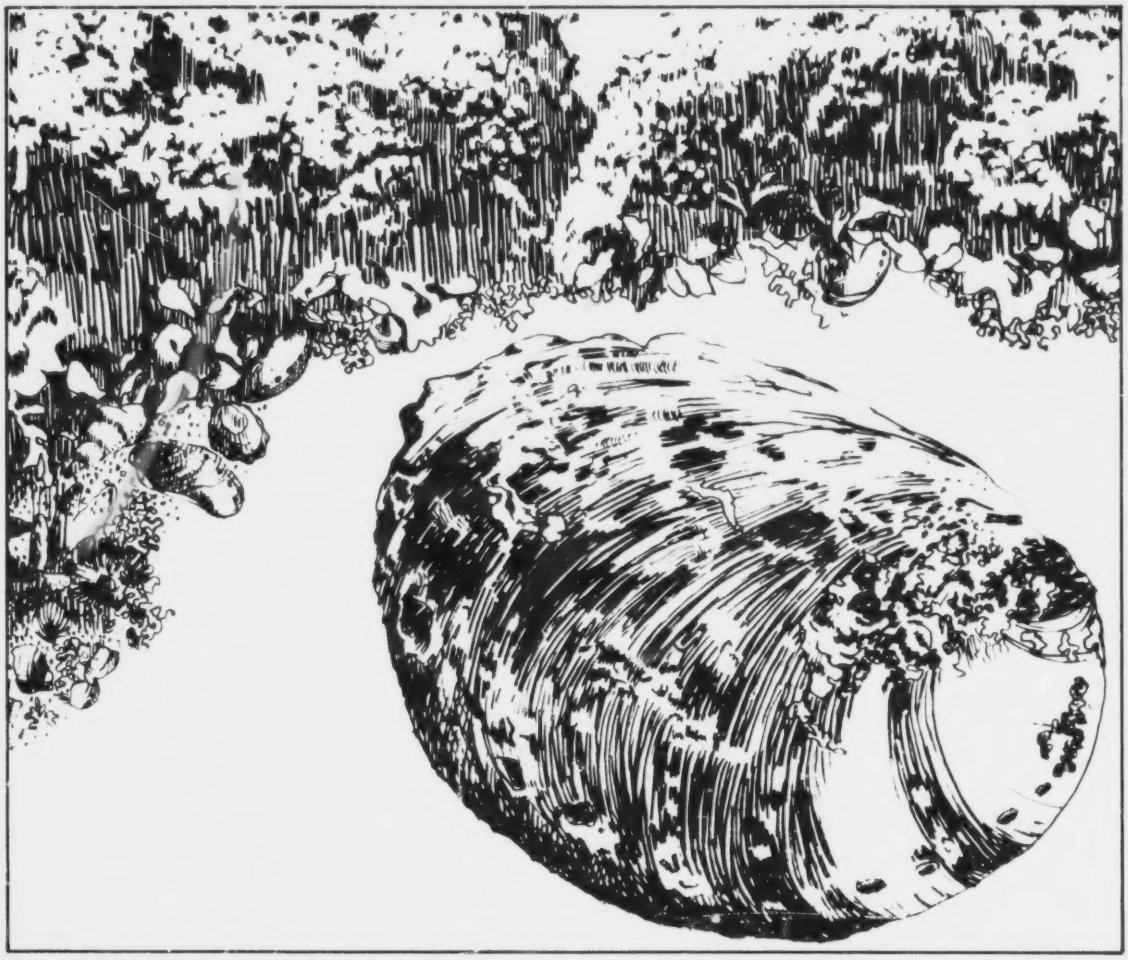
BLACK, GREEN, AND RED ABALONES



Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
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Biological Report 82(11.32)
TR EL-82-4
March 1985

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest)

BLACK, GREEN, AND RED ABALONES

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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Post Office Box 631
Vicksburg, MS 39180

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

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BLACK, GREEN, AND RED ABALONES

NOMENCLATURE/TAXONOMY

Scientific name . . . . . Haliotis cracherodii Leach
Preferred common name . Black abalone

Scientific name . . . . . Haliotis fulgens Philippi
Preferred common name . Green abalone

Scientific name . . . . . Haliotis rufescens Swainson
Preferred common name . . Red abalone

Class . . . . . Gastropoda
Order . . . . . Archaeogastropoda
Family . . . . . Haliotidae

REASONS FOR INCLUSION IN THE SERIES

All abalones belong to the genus Haliotis sensu latu, family Haliotidae. The 75 species known worldwide (Boolootian et al. 1962) are anatomically similar and all are adapted for attachment to hard substrates. Seven species are widely distributed along the coast of California (Cox 1962; Mottet 1978), of which several are important in the commercial and sport fisheries of the Pacific Southwest. (See Figure 1 for shell characteristics.)

GEOGRAPHIC RANGE:

Black abalone ranges along the Pacific coast from San Francisco Bay, California, to Bahia Santa Maria, Baja California Sur, Mexico, including the Coronado, Guadalupe, and all the Channel Islands. Generally, it is common to the south and rare to the north of Point Lobos (Figure 2).

The green abalone ranges from Point Conception to Bahia Magdalena, Baja California Sur, Mexico (Leighton et al. 1981), including the California localities of San Clemente, Santa Catalina, Santa Barbara, Anacapa, and Coronado Islands.

The red abalone ranges from Sunset Bay, Oregon, to Bahia San Bartolome, Baja California (29 N Lat.), including the Farallon and Channel Islands (Cox 1962; Leighton 1968). It is rare north of Shelter Cove, California.

MORPHOLOGY AND IDENTIFICATION AIDS

Black Abalone

The shell of the black abalone is comparatively deep and oval, its average shell length is about 115 mm (maximum 215 mm). The shell exterior is dark blue, black, or greenish black, usually smooth, and supports few or no encrusting organisms. Its round respiratory apertures (pores), which are flush with the shell surface, are about 3 mm in diameter. Usually five to nine pores are open at any one time, but in specimens from Baja California and Guadalupe Island, 11 to 14 pores may be open. The interior shell pigmentation is cream to silver pearl with pink and green iridescence. A columellar muscle scar is lacking. The outer edge of the shell protrudes over a nacreous surface forming a narrow, dark blue-black rim.

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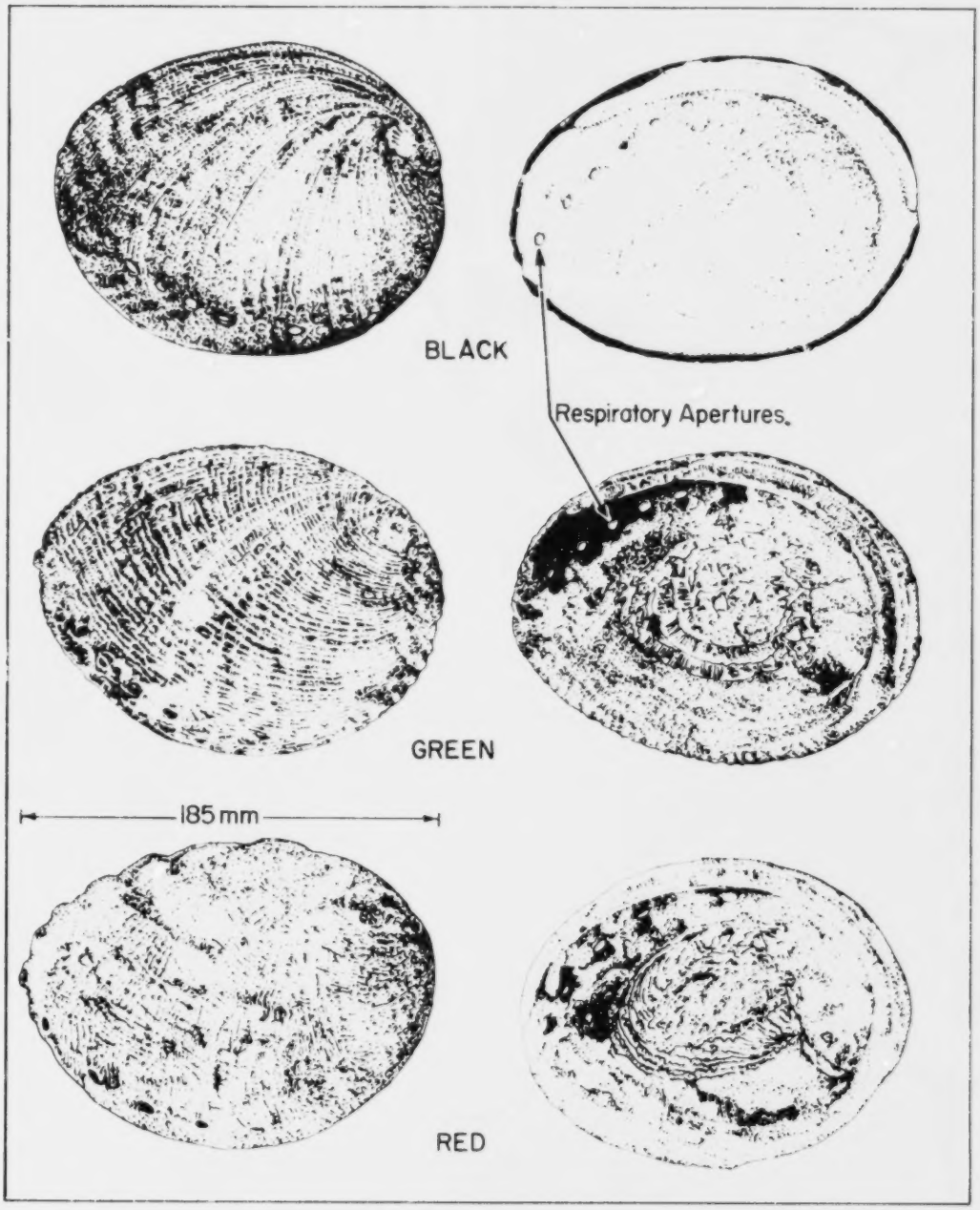

Figure 1. Shells of the black, green, and red abalones. Length measurement of typical shell is shown in lower left.

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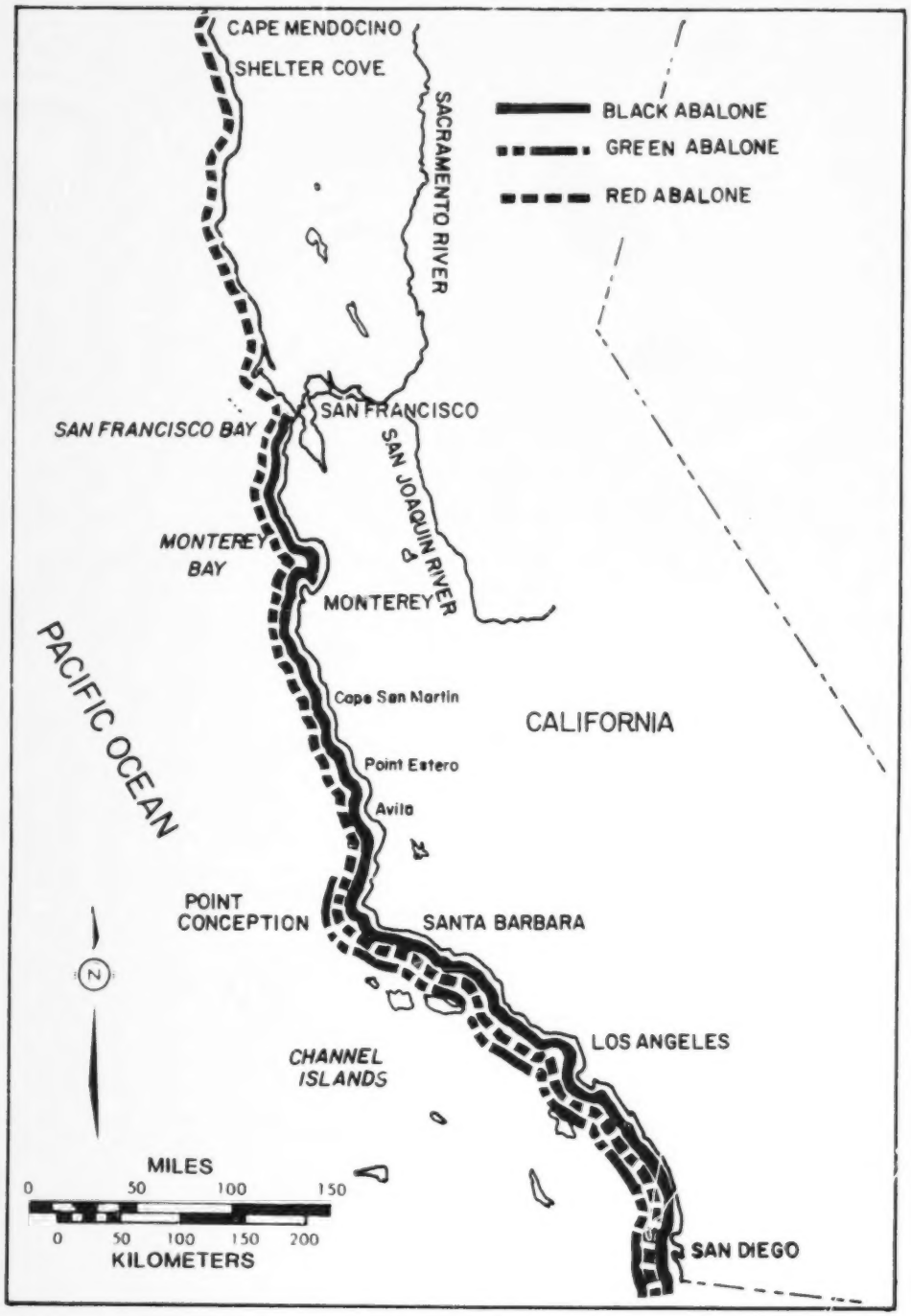

Figure 2. Coastal distribution of the black, green, and red abalones in California.

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The epipodium (dorsal rim of the foot) is smooth and black. Its upper edge is scalloped and bears short, slender tentacles that sometimes protrude slightly beyond the edge of the shell.

Green Abalone

The shell of the green abalone is oval; its average length is 175 mm (maximum 250 mm). The shell exterior is olive-green to red-brown and regular in form and sculpture with fine spiral ribs. The shell surface is often overgrown with encrusting invertebrates and algae. The circular respiratory apertures are about 5 mm in diameter and slightly raised; usually five to seven are open. The shell interior is smooth and strongly iridescent, having deep green, blue, and lavender shades and some black spots. A prominent, central, columellar muscle scar is present; the shell is considered to be the most beautiful of all abalones.

The epipodium of the green abalone is olive green with patches of brown. It is scalloped along the edge and small tuberculations give it a rough, frilled surface. Epipodial tentacles are grayish green, short, and thick, and project slightly.

Red Abalone

The red abalone is the largest of the abalones. The average shell length is about 220 mm (maximum 292 mm). Usually, three to four respiratory pores are open along the sinistral margin of the shell at a given time. The outline of the pores are oval and typically slightly elevated. The shell exterior is commonly lumpy, irregular, and red. The redness is conferred by red algae in the diet. The ostracal shell layer is typically dull brick red (Cox 1962). If red abalone feed on brown rather than red algae, the shell colors range from white to cream to green, depending on the particular brown algae being consumed (Leighton 1961; Olsen 1968a,b). The shell is often overgrown by sessile organisms that are common to the area. The shell interior is smooth and brilliantly iridescent with deep green and blue shades; green and black spots may also be present. The interior bears a large, prominent, central columellar muscle scar with rough texture. The outer lip of the shell extends over an inner nacreous surface forming a rim (red if the abalone has been feeding on red algae).

The epipodium and lateral portion of the foot are smooth and usually black; however, the epipodium of a second prominent phenotype has alternating dark and light vertical bars. The edge of the epipodium is scalloped; black epipodial tentacles can be extended beyond the edge of the shell. In some individuals, the upper edge of the epipodium is white. The epipodium protrudes beyond the edge of the shell when the animal is either relaxed or feeding.

LIFE HISTORY

Spawning and Maturation

Abalones lack evident sexual dimorphism and are dioecious, broadcast spawners. The sex of mature specimens can be determined by gonadal color (Cox 1962; Leighton and Boolootian 1963; Mottet 1978). The testis is usually white, yellow-cream, or beige; the ovarian tissue is dark green in black and red abalones and their larvae are conspicuously green. The green abalone has brownish-green ovarian tissue and produces brown eggs. Immature gonads are brown or brownish-gray -- the color of the hepatic tissue.

Gonadal histology has been described for the black abalone by Boolootian et al. (1962); for the green abalone by Sevilla et al. (1965) and Tutschulte (1976); and for the red

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abalone by Young and DeMartini (1970). All three species are histologically similar and there is no evidence of sex reversal. According to Leighton (1968) and Ault (1982), maturation of the gonads depends largely on the quality and quantity of available food, and to a lesser extent on temperature (within certain limits). Seasonal changes in the availability of food may determine the period of gamete production (Boolootian et al. 1962). Low food intake, combined with seasonally low ambient water temperatures, may cause suboptimal gamete development (Young and DeMartini 1970; Giorgi and DeMartini 1977; Ault 1982). All three species of abalones described here spawn primarily in spring and early summer.

Black abalone. Although black abalone usually spawn in late spring and early summer in both central California (Boolootian et al. 1962) and southern California (Leighton and Boolootian 1963), a minor second pulse of spawning in early fall was reported in central California by Webber and Giese (1969). Most black abalone longer than 44 mm were sexually mature near Point Dume in southern California (Leighton and Boolootian 1963). Gametogenesis is begun immediately after spawning is completed (Webber and Giese 1969).

Green abalone. Green abalone spawn from April through October in California coastal waters (Leighton 1979; Leighton et al. 1981; Tutschulte and Connell 1981) and as far south as Ensenada and Cedros Island in Mexico (Sevilla et al. 1965; Cota 1970). Green abalone off Santa Catalina Island may spawn twice a year (Tutschulte 1976). They mature sexually at 5 to 7 years of age at lengths of 80 to 120 mm (Tutschulte and Connell 1981). In laboratory experiments, green abalone became sexually mature and produced viable larvae as early as 1.5 years and lengths of 40 to 50 mm (Leighton et al. 1981). In California coastal waters, individual green abalone may produce from 100,000 to 6 million eggs per spawn (Tutschulte 1976).

Red abalone. Peak spawning of red abalone in the northern portion of their range coincides with spring benthic brown algal blooms. In northern California, the spawning season extends from April through July (Giorgi and DeMartini 1977; Ault 1982). . In southern California, they may spawn twice annually (Price 1974). Abalone living in the same environments have relatively uniform and similar gonadal development. Most red abalone in northern California become sexually mature when shell length is about 100 mm (Giorgi and DeMartini 1977). Abalone spawning for the first time may produce only a few thousand eggs, but older females may yield up to 6 million eggs (Giorgi and DeMartini 1977; Ault 1982). Red abalone reared in the laboratory became sexually mature and yielded viable larvae when about 40 mm long. Under optimum laboratory conditions, the fecundity of individual abalone can be doubled (Ault 1982). Gametogenesis of coastal red abalone is begun immediately after spawning and may be completed within 4 months (Ault 1982). Female red abalone first spawn in their third or fourth year of life and may continue to spawn for as long as 10 years. Necrosis of ova is suspected in geriatric females (Young and DeMartini 1970; Giorgi and DeMartini 1977). Insufficient nutrition inhibits egg production and in extreme cases the eggs may be resorbed (Giorgi and DeMartini 1977).

Larval Development

Larval development of the abalones is well-documented (Leighton 1974). Because the specific gravity of spawned eggs is greater than that of sea water, the eggs sink to the bottom. Upon fertilization, a membrane forms and larval development begins. The rate of embryonic development depends on temperature. Trocho-

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phore larvae hatch in 10 to 72 hours when the eggs are reared at water temperatures of 12 to 20 °C. Larvae are lecithotrophic. Trochophores and veligers are most abundant near the surface of the water.

Pigmentation of velar and visceral portions of the larvae may provide distinctive features for recognition of some species. Pigments derived from parental yolk appear to be retained by trochophore and veliger larvae of Haliotis (Leighton 1972). In the laboratory, veligers settle on the substrate when they are 5 to 14 days old. Settling of postlarvae on coralline red algae can be induced by substances released in the water by the algae (Morse et al. 1979). Metamorphosis into juveniles requires individual contact with red algae (Morse et al. 1980), yet there is some evidence that settling is a random phenomenon. Settlement (the crawling stage) marks the end of larval life.

Postlarvae and Juveniles

Postlarvae are the settled young up to 10 mm long. They are characterized by the loss of the velar cilia and operculum, and the pronounced development of the foot and shell (Leighton 1974; Mottet 1978). After 2 weeks, the postlarvae leave the coralline alga on which they have settled and attach to rocks, especially in crevices (Cox 1962). The postlarvae have a well-developed radula (rasping tooth structure) for feeding on bacteria and diatoms that grow as a film on the substrate. Once they have started to feed, they begin to deposit the peristomal shell around the lip of the larval shell aperture. The shell is depressed and grows in the form of an equiangular spiral. New shell material is deposited to a greater extent on the right side of the aperture, producing a shell with a right-handed whorl. The spiral becomes flattened and the shell becomes ear-shaped (Haliotis = sea ear), a form well suited for clinging.

Sensory tentacles have two ciliary lobes that create water currents over the ctenidia and epipodial tentacles, which function as chemosensory and tactile-sensory structures. When postlarvae are 1 to 3 months old and the shell is about 2 mm long, the first respiratory pore forms (Cox 1962) as the mantle separates along the sinistral margin of the shell opening and creates a notch (Leighton 1972). As growth proceeds, old pores are closed and new ones are formed one at a time along the growing margin of the shell. When the abalone is about 10 mm long -- now a juvenile -- it begins feeding largely on macroalgae, and to a much lesser extent on microflora (Cox 1962; Leighton and Boulootian 1963; Mottet 1978). Abalones are seldom seen in the open until they are 75 to 100 mm long (Cox 1962).

Habitat

Postlarvae, juveniles, and adults require hard substrate for attachment. The type and extent of rocky bottom materials largely determine abalone abundance. Optimum habitat consists of various combinations of ledges, cutbacks, depressions in stones, boulder piles, and other hard surfaces where food is abundant. Different microhabitats are necessary for the growth and survival of abalones of different sizes and ages, as are an abundance of particular algae species for food.

Black abalone live primarily in the rocky, mid-intertidal zone. Specimens larger than 90 mm tend to be sedentary and live under and on the sides of large rocks and in crevices. Smaller (< 90 mm) black abalone live primarily under boulders and in crevices. They move about more than the larger animals, presumably in search of food. The intertidal distribution of the species predisposes it to less predation from marine predators but to more predation from terrestrial predators (Morris et al. 1980).

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Green abalone are most abundant along rock headlands from the low intertidal zone to a subtidal depth of about 15 m. Headlands are exposed to high wave and current turbulence and abalones there are concentrated in crevices. The lower depth limits of abalones are governed by the severity of the wave action, by the availability of drifting red algae for food (Tutschulte 1976), and suitable water temperatures (Leighton 1974; Leighton et al. 1981). Juveniles also are abundant in areas where adults are abundant, especially in waters with strong currents and in crevices where coralline algae thrive. Postlarvae settle gregariously among adults (Tutschulte 1976; Morse et al. 1980). Most of the older juveniles and adult green abalone move frequently in search of food and protection (Tutschulte 1976).

In northern California, red abalone live in the lower intertidal zone, to a depth of about 6 m (J.D. DeMartini pers. comm.). In southern California they live subtidally out to depths of 40 m (Leighton 1968) but in northern California abalones longer than 75 mm live in crevices, under large boulders, and on exposed bedrock where sea otters (Enhydra lutris) are scarce. Smaller red abalone are cryptic, at least diurnally. Red abalone up to 20 mm long commonly live under clean boulders with veneers of inarticulate coralline algae. Red abalone up to 80 mm long commonly live in crevices. The seams, cutbacks and ledges in rock faces where algae are abundant provide optimal habitat for red abalone (J.D. DeMartini, Humboldt State University, California, pers. comm.). Red abalone seek locations where food is abundant and relatively easy to capture. The largest specimens tend to live in the choice locations (J.D. DeMartini, pers. comm.). Some abalone are relatively inactive and do not forage unless they are unable to catch sufficient drift algae; they then forage mostly among kelp stands.

GROWTH CHARACTERISTICS

The growth rates of the three abalone species are relatively uniform during their first few years (Leighton 1974). The length of most abalone is 1 to 3 mm at the end of 3 months, about 20 mm at the end of the first year of life, and 75 to 100 mm by the end of the third to fourth year. Growth in girth and weight increase as length increases. Black abalone are rarely longer than 175 mm, and the maximum length for red abalone is about 290 mm.

In southern California the average annual growth rate of the black abalone is about 20 mm over the first 4 to 5 years of life (Leighton and Boolootian 1963). In laboratory experiments, green abalone were as long as 30 mm by the end of their first year of life (Leighton et al. 1981). Tagged juvenile red abalone grew up to 48 mm in 1 year in central California (Cox 1962).

Growth rates of abalones fluctuate with the seasonal abundance of kelps (Cox 1962; Leighton and Boolootian 1963). Growth is rapid during the summer, when brown macroalgae are most abundant. Differences in growth rates also may reflect the differential nutrient quality of the available algae (Leighton 1972). In winter along the north coast of California, abalones may lose weight because of the paucity of brown algae for food. In northern California, about 80% of the annual growth of red abalone is during peak algal production in summer and fall (J.D. DeMartini, pers. comm.).

According to Hansen (1970), the rate of shell growth slows or stops during periods of accelerated gonadal growth, but more recent studies on red abalone in the laboratory indicate that shell growth and gonadal maturation may be simultaneous (Ault 1982). Gonadal development is fastest when the diet consists of giant kelp (Leighton 1968) or bull kelp (Ault 1982).

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Only a small percentage of abalones grow fast. Under optimal conditions in a laboratory culture, some juvenile red and green abalone grow as much as 50 mm in one year (Leighton et al. 1981; J. McMullen, Port Huememe, California, pers. comm.); however, the average is near 25 mm in the sea.

THE FISHERY

For comparison, the commercial catch data for abalone are compiled separately for southern California (Mexican border to Point Conception, Santa Barbara County, including the Channel Islands); central California (from Point Conception to San Francisco, including the Farallon Islands); and northern California (north of San Francisco to the Oregon border).

Commercial Fishery

Annual commercial landings of abalones have declined from 4.6 million pounds in 1966 to a low of 1 million pounds in 1979 (Table 1). The foot meat of the abalones is a highly prized delicacy, noted for its rich flavor. Commercial processing commonly involves separation of the body from the shell; the viscera and dark portions of the epipodium are trimmed, and the remaining light meat is sliced and pounded into steaks. The dorsum of the shells is sometimes cleaned with a strong acid; and the whole shell is then used as an ornament, or broken into smaller sections and polished for jewelry. Dwindling supplies have given this prized mollusk the distinction of being the highest priced domestically produced seafood in the United States. Historically, most of the commercial catch consisted of red abalone taken from central California coastal waters between Cape San Martin (Monterey County) and Avila (San Luis Obispo County); however, commercial landings of red abalone in central California have declined partly because of the expansion of the range of the highly predatory sea otter into old established abalone grounds. The other abalones (i.e., pink, black, green, and white), taken primarily from southern California, now make up two-thirds to three-fourths of the state abalone catch (Table 2). Commercial fishing for abalones is banned north of San Francisco.

Table 1. Commercial abalone landings and ex-vessel value in California, 1965-1982[a].

Year	Thousands of pounds[b]	Thousands of dollars
1965	4,576	$ 698
1966	4,964	915
1967	4,422	860
1968	4,475	1,124
1969	3,658	1,161
1970	2,901	948
1971	2,945	953
1972	3,093	1,248
1973	3,193	1,077
1974	2,595	1,299
1975	2,138	1,388
1976	1,733	1,125
1977	1,435	1,388
1978	1,295	1,530
1979	972	1,304
1981	1,092	2,096
1982[c]	1,184	2,192

[a] Includes landings of black, green, red, pink, white, threaded, pinto, and flat abalones. (No data for 1980).
[b] From California Marine Annual Fish Landings. Bulletins of the California Department of Fish and Game.
[c] Preliminary data.

The commercial fishery in southern California is regulated by a split season (closures during February and August) and by size limits. Fishing is regulated by limited entry. Commercial divers are restricted by types of gear, diving depth, and area

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Table 2. Annual commercial landings (pounds) of black, green, and red abalones at major ports of entry from 1972 to 1982[a]. (No data for 1980).

Year	Species	Central California			Southern California		Total
		San Francisco	Monterey	Santa Barbara	Los Angeles	San Diego	
1972	Black	-	-	852,615	130,008	32,269	1,014,892
	Green	-	-	3,228	259,814	161,786	424,828
	Red	33,098	150	944,119	19,745	107,350	1,104,362
1973	Black	-	-	1,334,095	468,915	109,939	1,912,949
	Green	-	-	3,206	123,599	29,999	156,804
	Red	21,715	-	568,770	5,260	68,174	663,919
1974	Black	-	-	793,696	33,631	18,069	1,145,396
	Green	-	-	3,047	99,758	18,758	121,563
	Red	40,043	45	639,004	10,102	61,866	751,060
1975	Black	-	-	594,152	91,167	2,109	687,428
	Green	-	-	3,053	140,624	27,250	170,927
	Red	53,001	848	624,148	8,889	55,883	742,769
1976	Black	-	-	267,379	85,686	3,686	356,751
	Green	-	-	1,231	88,659	30,599	120,489
	Red	62,953	1,365	604,275	9,121	61,907	739,621
1977	Black	-	-	360,718	83,605	18,978	463,301
	Green	-	-	3,409	65,529	28,519	97,457
	Red	97,672	-	382,756	12,328	44,694	537,450
1978	Black	27	-	272,004	136,979	10,966	419,976
	Green	-	-	3,903	74,227	14,912	93,042
	Red	84,331	-	369,839	6,025	28,952	489,147
1979	Black	-	-	190,715	108,786	20,864	320,365
	Green	-	-	4,115	41,431	13,548	59,094
	Red	47,057	105	359,768	5,796	21,247	433,973
1981	Black	606	-	363,701	133,259	11,334	508,900
	Green	940	-	2,423	45,551	14,961	63,875
	Red	53,422	736	300,834	3,319	66,875	425,186
1982[b]	Black	-	-	443,272	160,435	8,538	612,245
	Green	421	-	2,648	57,676	13,617	74,362
	Red	65,307	-	306,922	3,868	38,016	414,113

[a]From California Marine Annual Fish Landings, Bulletins of the California Department of Fish and Game.

[b]Preliminary data.

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boundaries. Commercial divers use the "hookah" system, which consists of a compressor and a surge tank with 300 to 500 feet of hose connected to a full face mask or the second stage of a scuba regulator. This system enables more than one diver to operate from a vessel and provides a more thorough inspection of crevices. Since the early 1950's the commercial diving fleet has increased from 75 vessels to about 210, an increase of nearly 180%. Although divers now use more efficient gear, they harvest only 50% of the amount that was consistently landed by the smaller fleet in the 1950's (Burge et al. 1975).

Sport Fishery

Since 1965, there has been a 400% increase in the number of recreational scuba divers who search for abalones in southern California, and a 250% increase in catch. The number of party boats designed for the use of scuba divers has also increased. These vessels now have sufficient range to take divers to all offshore islands in southern California. In central and northern California, there has been a more than 400% increase in shore-pickers and divers, and a doubling of the sport catch from Marin, Sonoma, and Mendocino Counties between 1965 and 1980. In central California the scuba season lasts 10 months. In northern California the catch is restricted to "free" divers (using mask and snorkel) and beach combers over a split 7-month season.

The daily possession limit in California is four abalones of any combination of species. Eight abalones are allowed in possession by sport-divers declaring a multi-day trip to offshore waters. Accessible red abalone populations in northern California are now at their optimum yield for sport purposes (Hardy et al. 1980).

Resource Status

Abalones are rare in the coastal waters between Avila and Monterey, California. The resurgence of the sea otter population along the central California coast coincided with a substantial reduction in commercial and sport catches for abalones. In the 1940's, the 200 miles of coastline between Monterey and Point Conception produced an annual commercial catch of 720,000 red abalone (Bonnot 1948), but densities of abalones and sea urchins fell drastically after the reestablishment of sea otters in the coastal waters of Monterey County in the early 1960's (Lowry and Pearse 1973). Abalone stocks within the sea otter's established range are too low for profitable commercial or sport fisheries. The relative changes in abalone density when sea otters became reestablished in 1970 near Point Estero are illustrated in Figure 3. This area supported a strong commercial fishery from about 1940 to 1970 (Hardy et al. 1980). The full impact of the sea otter on abalone fisheries was slow to be recognized by the public. Sea otters have depleted the most productive abalone grounds and are a threat to all abalone populations in California (Burge et al. 1975). Although the Marine Mammal Protection Act of 1972 categorizes the sea otter as a threatened species (Wyner et al. 1977), many authorities in California believe that it must be contained within a restricted range as a necessary prerequisite to the development of a viable management plan for abalone resources in California (Wyner et al. 1977; Hardy et al. 1980).

A metal bar of about 12 inches in length, 1-1/2 inches wide, and 1/4 inch thick is the standard commercial and sport diving tool used to collect abalones. The tool is used to break the suction-vacuum created by the abalone's foot against the substrate. In southern and northern California (areas outside the sea

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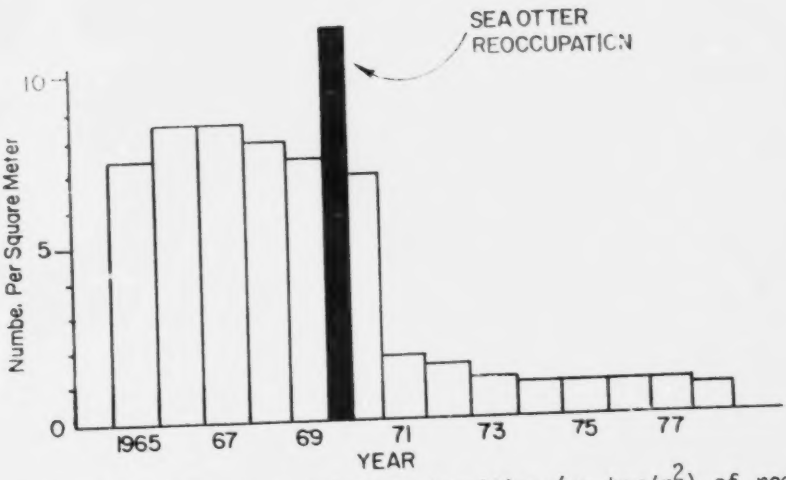

Figure 3. Average population densities (number/m^2) of red abalone at Point Estero, California, 1965-1978 (from Hardy et al. 1980).

otter's range), a high percentage of the abalones that are removed from the substrate by commercial and sportdivers, then replaced because they are found to be below legal size, die because of injury or improper replacement. Abalones are hemocoels, i.e., the blood sinuses pass through the foot. Metal picking bars sometimes sever these blood sinuses, causing a loss of blood pressure and fluids. About 50% of the abalones injured (but not removed) by picking bars are likely to die (Burge et al. 1975). Abalones not securely attached to the substrate also become easy prey for fishes. General declines in standing stocks of abalones may be caused by catches of abalones below legal size and by habitat degradation (Hardy et al. 1980).

In 1984, studies are being conducted to determine the feasibility of rearing 1- to 2-year-old abalones of several species in the laboratory and transplanting them into suitable habitats where populations have declined. Seeding abalone habitat with juveniles may prove to be an effective means of repopulating formerly productive waters (Leighton et al. 1981).

ECOLOGICAL ROLE

Food and Feeding Habits

Abalones are herbivores that feed largely on brown and red algae, somewhat in proportion to its availability. Densities are often high in locations with abundant algal drift or *in situ* kelps. Studies of the food and feeding have been reported for black abalone by Leighton and Boolootian (1963), for green abalone by Leighton (1966), and for red abalone by Leighton (1966, 1968) and J.D. DeMartini (pers. comm.).

Newly hatched abalone have enough yolk to last for several days. By the time the larva settles, its radula has developed sufficiently to enable the ingestion of microalgae less than 10 micrometers long. Abalones less than 10 mm long usually subsist on a diet of sessile pennate diatoms such as *Navicula* and *Nitzchia*, and some bacteria (Leighton 1972; Mottet 1978).

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Small abalones (less than 5 mm long) graze primarily on benthic microflora (Leighton et al. 1981; Olsen 1968b). Although small juveniles do not feed directly on kelp, kelp beds provide cryptic refuges that enhance survival of abalones. The young often grow well in waters unsuitable for adults. Although small juveniles prefer to feed on seaweeds with thin fronds, juveniles as short as 1 cm long can eat the same food as adults. When kelp is sparse, diatoms may form a large part of the adult diet.

Coastal waters inhabited by abalones off California and Baja California flourish with the Phaeophyta (Table 3). The production of algae is highly seasonal and the amount of algae being consumed usually reflects its availability (J.D. DeMartini, pers. comm.). In northern California waters in late fall, annuals begin to disintegrate and perennials die back. The abundance of food then drops sharply and remains low until the following spring. At the same time, the growth of the abalones drop sharply (Leighton and Boolootian 1963; J.D. DeMartini, pers. comm.).

Table 3. Common brown and red algae (kelp) in nearshore waters of southern California (south of Point Conception) and northern California (Point Conception to Oregon border).

Southern California	Northern California
Division Phaeophyta (Brown algae)	Division Phaeophyta (Brown algae)
Cystoseira osmundacea	*Alaria marginata*
Desmarestia ligulata	*Costaria costata*
Egregia menziesii	*Desmarestia ligulata*
Eisenia arborea	*D. viridis*
Halidrys dioica	*Dictyoneurum californicum*
Laminaria sinclarii	*Egregia menziesii*
L. farlowii	*Hedophyllum sessile*
Macrocystis pyrifera	*Laminaria dentigera*
Pelagophycus porra	*L. sinclarii*
Pterygophora californica	*Lessoniopsis littoralis*
	Macrocystis pyrifera
	M. integrifolia
	Nereocystis luetkeana
	Postelsia palmaeformis
	Pterygophora californica
Division Rhodophyta (Red algae)	Division Rhodophyta (Red algae)
Gelidium sp.	*Botryoglossum farlowianum*
Gigartina sp.	*Gigartina* sp.
Lithothamnion sp.	*Hymenena* sp.
Plocamium coccineum	*Tridaea* sp.
Rhodymenia sp.	*Lithothamnion* sp.
	Porphyra sp.
	Prionitis sp.
	Rhodymenia sp.
	Schizymenia sp.

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Since some species of algae are more nutritious than others, somatic and gonadal growth is influenced by the species of algae eaten (Leighton 1968). The coincidence of gonadal growth and food supply has been observed for both the green abalone (Leighton et al. 1981) and the red abalone (Leighton 1974; Ault 1982). Both ocean and hatchery-reared adults can be spawned artificially in the laboratory every month of the year if sufficient food is available. Grazing can be selective under certain conditions, and food toughness may influence choice. For example, the more resilient, denser algae are eaten at a slower rate than the tender tissues (Leighton 1966); however, selectivity tends to disappear when food is scarce. Although bits of drift kelp are an important source of food, attached kelp also is eaten.

Abalones feed by raising their shell and extending their epipodium (Cox 1962). When a piece of drift touches the epipodium, the abalone turns toward the food and grasps it with the highly prehensile anterior lobes of the foot. By creating rhythmical contractions of the foot the algae is drawn under the anterior half of the foot (D.L. Leighton, World Research, Inc., San Diego, CA; pers. obs.). Water current, light, and other stimuli also elicit feeding behavior (Olsen 1968a).

The summer feeding posture of abalones could cause easy detachment when food is scarce. Thus, abalones are commonly depressed onto rock surfaces with their epipodial tentacles extended during winter. These animals feed only when contacted directly by drift algae.

Black abalone. The black abalone feeds mostly on brown algae, and to a lesser extent on red algae. The smaller abalones (less than 20 mm long) graze on diatom films and coralline algae, but larger ones subsist on fragments of algae brought in by waves and currents. Under laboratory conditions black abalone have shown a preference for the brown alga Egregia, but Macrocystis produced the most rapid growth. To some extent, shell color varies with the diet (Leighton 1961; Olsen 1968a,b).

Green abalone. Green abalone eat brown algae proportionate to its abundance in the algal drift. The larger brown algae Macrocystis and Egregia predominate in the diet (Leighton 1966) and produce the best growth (Leighton 1979). However, the green abalone strongly prefers the red algae Gelidium, Pterocladia, Plocamium, and Gigartina. Red algae are three times more abundant in the diet of the green abalone than they are in the algal drift (Tutschulte 1976).

Red abalone. Adult red abalone mainly eat brown macroalgae. Juveniles (less than 20 mm long) graze on diatom films or other sessile microscopic plants, and the shell's dorsum may be pink, bluish-green, or white. Pigmentation of the ostracum reflects the diet in nature (Leighton 1961). When red algae become predominant in the diet, either as consumed kelps or as epiphytic growths on consumed kelps, the ostracum of the abalone becomes reddish. Individuals alternately fed red and brown algae show alternate banding of red and white. Color sequences in the shells may be used as a key to botanical succession in the home area of the respective animals. Yearly color sequences indicate growth rate relative to season and diet (Olsen 1968a). At Point Cabrillo, Mendocino County, the annual and seasonally abundant species Alaria marginata and Desmaresetia ligulata var. ligulata account for more than 65% of the food observed being eaten (J.D. DeMartini, pers. comm.). South of San Francisco, kelp beds of Macrocystis and Nereocystis dominate the diet (Cox 1962; Leighton 1968). These kelps are rich in protein and carbohydrates that are highly digestible (Leighton 1968).

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Competition and Predation

Competition between abalones and sea urchins in rocky nearshore waters is intense. The sea urchin Strongylocentrotus franciscanus is distributed throughout the range of the abalones. Abalones and urchins occupy the same general habitats and eat much the same food (Leighton 1968), but the maintenance demands of abalones are three to four times greater than those of sea urchins (Leighton 1968). The apparent negative kelp growth affected by urchins destroys recruiting sporophytes and greatly reduces abalone food production (Leighton 1966, 1968). Abundant sea urchins may completely denude kelp plants. In shallow water where sea urchins are scarce, kelp and other algal growth is usually lush.

In southern and central California, the small dark-purple shrimp Betaeus harfordi is a commensal in the mantle cavity and the mantle groove of green and red abalones; it positions itself with its head near the abalone's mouth. There is a direct correlation between the size of the abalone and the size of the commensal shrimp (Morris et al. 1980). Boring organisms living in carbonate matrices often infest the shells of abalones. The boring sponge Cliona celata initially attacks near the spire of the abalone shell, then riddles the host, reducing the shell to a fragile skeleton (Hansen 1970). A small clam, the abalone piddock (Penitella conradi) bores at right angles into the dorsal aspect of the abalone shell (Cox 1962). As the clam penetrates the shell and approaches the inner surface, the abalone secretes nacre locally over the inner surface of the shell, forming a blister pearl (Hansen 1970).

The mortality of abalones is probably greatest in the planktonic stages. Those that survive to live on the benthos are preyed upon by sea stars, crabs, fishes, octopuses, sea otters, and man. Some asteroids can extend their stomachs completely over large abalones (185 mm long) and digest them by secreting gastric juices through the respiratory pores of the abalone. Abalone display active escape responses in contact with, or in proximity of, the sea stars Pycnopodia helianthoides and Pisaster ochraceus (Montgomery 1969). Abalones attempt to escape by making a galloping retreat coupled with repeated 180 degree rotations of the shell. By extending the epipodium over the shell surface the abalone applies a copious amount of mucus to the shell, which helps prevent the tube feet of the sea star from fastening to the shell (Montgomery 1969). The number of actual accounts of sea star predation on abalones in relation to abalone abundance is so slight that asteroids are probably not a serious threat under usual conditions; however, under severe oceanic conditions, when abalones are prone to being injured by rolling boulders, asteroid predation may be commonplace. The shifting or disturbance of boulders in abalone habitat causes an immediate but usually temporary movement of most juvenile and adult abalones.

Fishes and sea otters sometimes catch abalones that have raised their shells to catch drift algae. Abalones may be dislodged by a sharp bump from fishes like the California sheephead, Semicossyphus pulcher; cabezon, Scorpaenichthys marmoratus; kelp greenling, Hexagrammos decagrammus; kelp bass, Paralabrax clathratus; or barred sand bass, P. nebulifer. They may also be dislodged by a sea otter or a bat-ray, Myliobatus californica, which pries them loose with the lower jaw.

Where abundant, sea otters are the major predators of large abalones, preferring them over all other foods (Hardy et al. 1980; Hines and Pearse 1982). The sea otters use rocks to break the top of an abalone shell, exposing the soft body parts. Because of this intense predation, abalone

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populations are restricted in distribution to cryptic microhabitats and older abalones are relatively scarce (Hines and Pearse 1982). Octopuses are capable of pulling small abalones from the rocks, or drilling through the shell of abalones of all sizes. Man is a long-time predator on abalones (Cox 1962).

ENVIRONMENTAL REQUIREMENTS

Temperature

The vertical and latitudinal distribution of abalones is most closely related to water temperature (Cox 1962; Leighton 1974). The distribution of juveniles and adults of each abalone species corresponds well with thermal tolerances observed in the laboratory (Leighton 1974). Their tolerance increases with age. Larvae that have the best chance of survival live in water(s) with optimum temperature and settle in areas where temperature changes are not excessive (Leighton 1974).

The thermal optima for the red abalone is between 14 and 18°C (Leighton 1974). The optimal temperature for egg fertilization is apparently 15 °C (Ebert and Hamilton 1983). Red abalone eggs develop normally within a temperature range of 10-23 °C, but optimum larval growth is at 13.5-20°C. At 18 °C, larvae settle in about 5 days. Larval growth is temperature dependent; only larvae reared between 14 and 18 °C reached the advanced post-larval stages (Leighton 1974). The red abalone feeds at temperatures of 7 to 22 °C, but maximum feeding is between 13 and 18 °C (Leighton 1968). Growth was fastest at temperatures between 15 and 20 °C and was only slightly less at 12.5 °C (Leighton 1974).

The black abalone is an intertidal species that lives over a broader latitudinal range than red or green abalones, yet the thermal requirements of red and black abalones are similar (Leighton 1974).

Larval and juvenile green abalone grow and survive well at 20 to 28 °C (Leighton et al. 1981), but the optimum temperature is between 18 and 24 °C (Leighton 1974). The time required for green abalone larvae to reach the settling stage varies from 3.5 days at 24 °C to 12 days at 14 °C. Larvae incubated at 12 °C failed to settle within 2 weeks (Leighton et al. 1981). Young laboratory-reared green abalone grew fastest at temperatures of 22 to 28 °C. When postlarvae were reared at near optimal thermal and feeding conditions, they formed the respiratory pore in about half the time required by other California abalones (Leighton 1974). The "notch stage" was reached in some rapid-growing green abalones within 30 days after fertilization. Juveniles usually live beneath rocks and in crevices in the lower intertidal zone where they are exposed to temperatures of about 12 to 26 °C. In one experiment, the growth rates of juveniles in thermal effluent (22-28 °C) were increased twofold over those reared at ambient temperatures (14-20 °C). Increases in shell growth are linearly dependent on temperature (Leighton et al. 1981). Green abalones grow fastest in water at about 26 °C. The optimal thermal range for somatic growth declines with age, corresponding with the lower temperatures in the sublittoral areas occupied by adults (Leighton et al. 1981).

Depth

The black abalone lives higher in the intertidal zone than any other California species. It ranges from the mid-intertidal zone to about 3 m below mean low tide.

The habitat of green abalone usually extends from the intertidal zone to a depth of about 20 m; however, few of the animals live below 10 m. They are most abundant at depths of 2 to 3 m below mean low tide

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in areas of high turbulence, strong surge, and suitable crevice refuge.

In northern California, red abalone inhabit water from 0 to 35 m deep, but concentrate in water 1 to 6 m deep. In Morro Bay, central California, the red abalone lives in intertidal waters up to 30 m deep (maximum concentrations are between 5 and 17 m), and as far as 2 miles offshore if there is abundant rocky substrate and food supply (Cox 1962). Near San Diego, California, red abalone usually live in water 8-40 m deep; maximum concentrations are between 12 to 15 m. Although red abalone are relatively abundant off southern California and Mexico, they are seldom encountered at depths less than 12 m (Cox 1962), and are usually restricted to rock bottoms 10 to 30 m deep (Leighton 1968). This depth distribution correlates with an extended photic zone, generally higher algal production, and more suitable temperatures at greater depths.

Other Environmental Requirements

In waters north of San Francisco, abalones occupy a narrow coastal band, restricted to the nearshore waters where either drift or attached kelp is available for food. Along the coasts of Sonoma and Mendocino Counties in northern California, abalones are common below the algal zone, especially along the bottoms of surge channels, and are not always near attached algae. The availability of drift macroalgae varies daily. Water movement is essential for transporting food that abalones can catch (Olsen 1968a). Abalones in deep water (20-30 m) live in channels serving as funnels for drift kelp transported from shallow water. In southern California these underwater channels bear a strong resemblance to terrestrial desert washes (J.S. Ault, author, pers. obs.). Along a coastline with adjacent surge channels, abalones are characteristically further offshore. This more seaward distribution is correlated with greater kelp abundance there, either adrift or attached (Olsen 1968b). Abalones are scarce where channels widen and currents become diffuse.

Although much rocky habitat is common along the coasts of Humboldt and Del Norte counties in the extreme north of California, these coastlines are highly exposed, and abalones are scarce north of Shelter Cove, Humboldt County. In winter, overlying waters are sometimes excessively turbid due to high freshwater inflow. Unusually large freshwater inflows near river mouths may kill all abalones in the immediate vicinity (Bonnot 1948). If the water is turbid too long, most brown algae in waters 6 m or less below mean low tide are excessively shaded and die. In addition, excessive exposure to swell and sand abrasion inhibits sporophyte recruitment and reduces the production and availability of algae. The shifting of sand by strong bottom currents sometimes smothers large numbers of abalones (Bonnot 1948). The deepest that abalones are found north of Shelter Cove is about 6 m; consequently most of their habitat is subtidal. They inhabit even shallower water if food is abundant there.

Abalones are relatively scarce in the two most northern counties of coastal California because food and surge channels are both scarce. Surveys off the coast of San Diego and Santa Barbara revealed that small rocks encrusted with patches of coralline red algae frequently served as nursery grounds for juvenile red abalones and other species of Haliotis (Morse et al. 1980). These areas are scarce in the two northernmost counties of northern California. Abalone larvae there may have drifted from the more productive waters to the south (J.D. DeMartini, pers. comm.).

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16. Abstract (Limit: 200 words)

Black, green, and red abalones (Haliotis cracherodii, H. fulgens, and H. rufescens, respectively) are of commercial and ecological importance and are distributed widely along the California coast. The abalones are morphologically similar; species are distinguished by particular shell sculpture, color, and body characteristics. Their latitudinal and bathymetric distribution is stratified and most closely related to temperature. Small juveniles eat mainly microflora; adults eat primarily drift macroalgae, preferring specific brown or red algae, when available. Spawning occurs during summer; gonad ripening depends on food quality and quantity and water temperature. Larvae are lecithotrophic and remain planktonic for periods of 5 to 14 days after hatching; settling is substrate specific. Postlarvae and adults require hard substrate for attachment. Juveniles are cryptic, adults usually more exposed. Growth rates are similar, although maximum size varies with species. Increases in shell length and body weight correlate positively with food abundance and temperature. Below depths of 6 m, sea urchins are major competitors for food and space. Predation by invertebrates is low. Decreased abalone production from central California is associated with range expansion and increased predation by sea otters, the major source of abalone mortality. General declines in California landings are due to mortality from improper picking and replacement, habitat degradation, and perhaps overfishing. Commercial and sport diving efforts have increased sharply, whereas annual landings of abalones declined from 1965 to 1982.

17. Document Analysis a. Descriptors

Shellfish
Distribution
Age
Food habits
Growth

b. Identifiers/Open-Ended Terms

Predation
Life history
Habitat requirements
Black abalone
Haliotis cracherodii
Green abalone
Haliotis fulgens
Red abalone
Haliotis rufescens

c. COSATI Field/Group

18. Availability Statement

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